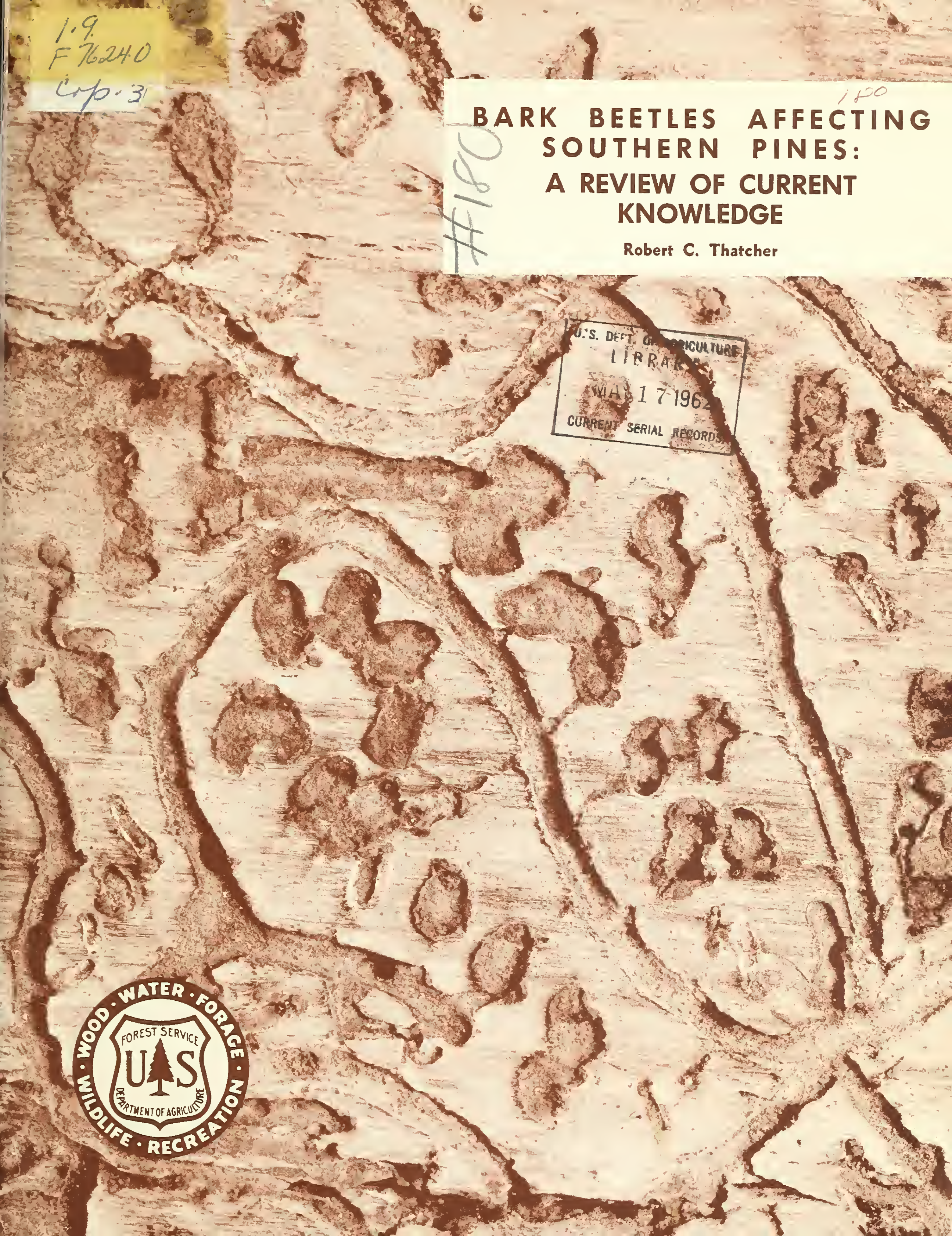

BARK BEETLES AFFECTING SOUTHERN PINES: A REVIEW OF CURRENT KNOWLEDGE

Robert C. Thatcher

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FOREWORD

Bark beetles are generally considered the most destructive insects affecting southern pines. They have received considerable attention from entomologists and foresters, but much of the accumulated knowledge is not readily available in publications. Thatcher has performed a valuable service by assembling, organizing, summarizing, and interpreting information from many sources.

This compilation and analysis of existing knowledge shows the need for much additional research. Some facets of the broad problem are pointed out, and work on these will undoubtedly suggest many more. It is hoped that this paper will stimulate other entomologists to undertake studies that will contribute to eventual solution of the bark beetle problem.

Bark-beetle control methods now in use are little more than stop-gaps that may keep losses from becoming catastrophic. Very little is definitely known about the physical and biological conditions that permit outbreaks to develop or cause them to diminish. Such information can only be obtained by painstaking study of each insect, its natural enemies, and the physical and biotic factors that affect its host trees.

Entomologists, foresters, students, and others will find this a useful reference.

L. W. Orr

Contents

BARK BEETLES AFFECTING SOUTHERN PINES: A REVIEW OF CURRENT KNOWLEDGE

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Bark beetles are the most destructive insects of southern pine forests, annually killing millions of board feet of sawtimber and large volumes of pulpwood.

Five species are responsible for most of the loss—the southern pine beetle (*Dendroctonus frontalis* Zimm.), the three southern *Ips* engraver beetles (*Ips calligraphus* Germ., *Ips grandicollis* Eichh., and *Ips avulsus* Eichh.), and the black turpentine beetle (*Dendroctonus terebrans* (Oliv.)).

The southern pine beetle causes the most spectacular damage by epidemic attacks which destroy large volumes of pine in localized areas at infrequent intervals of time. The southern *Ips* beetles and black turpentine beetle, on the other hand, are widely dispersed, seldom killing more than a few trees in one location except during very adverse weather. Over the years, however, they probably destroy more timber than does the southern pine beetle *(60, 68)*.[2]

Pine bark beetles are found in a wide variety of environments over the South, and the species differ greatly in their life histories and their effects on the host trees. Weakened or dying trees, rather than healthy green ones, may be considered their normal environment. In such material they are generally innocuous, though they may hasten deterioration. It is their ability to leave their normal hosts and destroy apparently healthy trees that makes them important to foresters and entomologists.

All species of pine native to the southern states *(11, 12, 15, 53, 55,56, 66, 92)* are attacked. In northerly parts of the bark beetles' range *(59, 79)* *Picea* and other species of *Pinus* also are hosts.

Table 1 summarizes the outbreaks that have been recorded in the southern region since 1882. Although the early reports often indicated only the gross area affected, the table nevertheless gives some indication of the damage from the more serious outbreaks. Since 1950 there has been an attempt to record endemic as well as epidemic losses, but scattered attacks, primarily by *Ips* and black turpentine beetles, are still generally overlooked. Perhaps the best estimate of total damage is in the U. S. Forest Service's TIMBER RESOURCES FOR AMERICA'S FUTURE *(124)*. On the basis of data from Federal, State, and private foresters, the compilers estimated that bark beetles caused more than 400 million board feet of mortality and growth loss in southern pine forests during 1952. That was not a year of heavy beetle activity; losses would be much greater during epidemic years.

SPECIES CHARACTERISTICS

The outstanding biological characteristic of the bark beetle is the secluded life of all stages. The beetles spend most of their lives in the cambium and inner bark of their hosts. Construction of egg galleries by the adults and subsequent mining by larvae girdle the tree. This girdling, plus the introduction of associated fungi, kills the host tree.

Mature adults of all species are cylindrical, ranging from reddish-brown to black in color and from 1 to 8 mm. in length. Antennae are capitate. Larvae have white bodies and brown head capsules, and are legless. *Dendroctonus* adults can be distinguished from *Ips* by their rounded elytral declivity, as contrasted with the concave declivity of *Ips*.

[1] Nacogdoches Research Center, maintained in cooperation with Stephen F. Austin State College, Nacogdoches, Texas.
[2] Italic numbers in parentheses refer to Literature Cited, page 21.

Table 1.—*Recorded pine bark beetle outbreaks in the South*

Date	General location	Volume loss or area of infestation	Reference source
	SOUTHERN PINE BEETLE		
1882-85	Texas		*(53)*
1890-92	Central Atlantic States	75,000 sq. mi.	*(53)*
1902-05	North Carolina, Georgia		*(26)*
1907-08	Virginia		*(26)*
1910-12	Entire South		*(26, 58)*
1913-16	Tennessee, Virginia	200 sq. mi.	*(26)*
1920	Entire South	117,000 MBF	*(1)*
1922-24	Entire South		*(26)*
1926	Texas		([1])
1929	North Carolina, Virginia		*(87)*
1931-32	Entire South		*(21)*
1937-38	Virginia		*(40)*
1939	Texas		([1])
1949-51	Texas	200,000 MBF	*(61)*
1952-55	Alabama	4,330 MBF	*(110, 112)*
	Mississippi	75,000 MBF	*(110)*
1957-58	South Atlantic	53,200 MBF	
	Coastal States	138,600 cords	*(72)*
	Louisiana		*(116)*
	Mississippi	1,204 MBF	*(118)*
	Texas		*(120)*
1958-	Texas	10,000 MBF	([2])
	***IPS* BEETLES**		
1922-24	Entire South	100,000 MBF	*(85)*
1925	Florida		*(21)*
1931-32	Entire South		*(21)*
1949-51	Florida	20,850 MBF on 74,000 acres	*(69)*
1952-55	Alabama	1,000 MBF	*(112)*
	Arkansas	27,750 MBF	
	Mississippi	25,000 MBF	*(110)*
	Texas	4,507 MBF	([3])
	South Atlantic	502,400 MBF	
	Coastal States	728,300 cords	*(72)*
1956	Arkansas, Louisiana, Oklahoma, Texas	100,000 MBF	([3])
	BLACK TURPENTINE BEETLE		
1949-51	Louisiana	3,000 MBF, 14,000 cords on 125,000 acres	*(65)*
1952-55	Louisiana	1,000 MBF	*(112)*
	Mississippi	75 MBF	*(112)*
	Texas	263 MBF	([4])
	South Atlantic Coastal States	107,000 MBF, 31,200 cords	*(72)*
1956	Texas	98 MBF	
1957-58	Louisiana	2,000 MBF	*(119)*
	Texas	105 MBF	([4])

[1] Personal communication with Kirby Lumber Corporation, Silsbee, Texas.
[2] Personal communication with Texas Forest Service.
[3] Personal communication with Kirby Lumber Corporation, Silsbee, Texas, Champion Paper and Fibre Company, Huntsville, Texas, and Texas National Forests, Lufkin, Texas; and estimates by Southern Forest Experiment Station.
[4] Personal communication with Champion Paper and Fibre Company, Huntsville, Texas, and Texas National Forests, Lufkin, Texas.

The earliest signs that a tree is under attack are white, yellow, or reddish-brown pitch tubes on the bark, or reddish boring dust or white resinous particles (in the case of the black turpentine beetle) in the bark crevices or on foliage of understory plants. Such particles can often be seen in spider webs near the base of the trees.

Later, as the broods develop, foliage becomes discolored, bark sloughs from the upper stem (southern pine beetle and *Ips* beetles), and white boring dust from ambrosia beetles may accumulate around the base of the tree. The foliage of trees infested by southern pine or *Ips* beetles may turn pale green to yellow in 2 to 3 weeks and brownish to red in 4 to 6 weeks during warm months *(11, 12, 66)*. With the black turpentine beetle, fading usually begins 4 to 8 or even 12 months after initial attacks *(98, 99, 102)*. Crowns discolor uniformly on trees infested by all beetles except *Ips avulsus*, which normally causes discoloring from the top down.

Occasionally the workings of associated insects are confused with those of the bark beetles. Some general features that distinguish bark-beetle attacks from those of wood borers, ambrosia beetles, and other associates are listed in Table 2.

Table 2.—*Features that distinguish workings of southern pine bark beetles from those of associated insects*

Southern pine bark beetles	Wood borers	Pinhole borers	Other associated insects [1]
Distinct pitch tube or fine reddish boring dust or white resinous boring particles created by entering adults.	Adults do not enter through bark.	Attack associated with dead portions of tree; small holes through bark; fine white or yellowish boring particles.	No pitch tubes and few boring particles.
Characteristic egg galleries cut by adults in cambium-phloem.	Eggs in niche cut in outer bark or placed in bark crevice; no egg gallery.	Distinct egg gallery cut in outer sapwood and stained black by ambrosial fungi.	Few construct egg galleries.
Egg galleries of *D. frontalis* and *D. terebrans* tightly packed with fine boring dust; galleries of *Ips* usually clean.		No boring particles in egg gallery; ambrosial fungus on gallery walls.	Egg galleries of secondary bark beetles with or without boring dust depending on species; termite galleries with cement-like deposit.
Larval mines generally perpendicular to egg gallery; located in cambium-phloem or cambium-phloem-middle bark; packed with fine boring dust.	Initial larval mines meander in cambium-phloem and surface of sapwood; subsequent mining in sapwood for several species.	Larvae usually develop and feed on ambrosial fungi in adult galleries.	Location and orientation of larval mining varies by species or is lacking.
Pupation in individual cells in cambium-phloem or phloem-middle bark.	Pupation in frass-plugged mine in sapwood, or in frass-surrounded cell immediately below bark.	Pupation in sapwood cells.	Pupation in sapwood, beneath or in bark.
Emergence of adults creates shothole effect in bark.	Emergence through relatively large, scattered, circular or oval holes.	Emergence frequently after bark has sloughed off.	Emergence holes less numerous and of size varying with species.

[1] Secondary bark beetles, scavengers, predators, wood feeders other than borers.

Southern Pine Beetle

Because beetles are hard to find readily except during epidemics, and no methods for maintaining laboratory populations have been developed, the southern pine beetle is difficult to study. Its frequent scarcity is illustrated by Blackman's failure to find specimens during 7 months of collecting in Mississippi during 1922 *(15)*. Nevertheless, a fairly complete idea of its normal life history, and some of its biological characteristics, can be constructed from work done by Hopkins from 1890-1910, by Blackman and Snyder in the early 1900's, by MacAndrews, Beal, St. George, and others in the 1920's and 1930's, and by Fronk, Osgood, and others since 1945.

Adults range from 2.2 to 4.2 mm. in length (table 3). The front of the adult head has a distinct longitudinal groove bordered by a nar-

Table 3.—*Comparative characteristics for southern pine bark beetles*

Characteristics	*Ips*			*Dendroctonus*	
	avulsus	*grandicollis*	*calligraphus*	*frontalis*	*terebrans*
Adult length (mm.)	2.1-2.6	3.0-3.8	4.0-6.0	2.2-4.2	5.0-8.0
Adult width (mm.)	.8-1.0	1.1-1.4			
Adult color	Reddish-brown to black	Reddish-brown	Reddish-brown to black	Brown or black	Dark-brown to black
Teeth on elytral declivity	4	5	6	None	None
Elytral declivity	Moderately excavated	Strongly excavated	Deeply excavated	Convex	Convex
Portion of tree usually attacked	Limbs and tops under 6 inches in diameter	Upper trunk, limbs of larger trees	Trunk	Middle and lower trunk	Base of trunk, or stump
Pitch tubes	Frequently none	Small, pink or red-brown	Small, pink or red-brown	Small, white, yellow or red-brown	Large, white to deep pink
Boring particles	Fine, red-brown	Fine, red-brown	Fine, red-brown	Fine, red-brown	Coarse, white or red resinous particles
Egg gallery—shape	Irregular, longitudinal	H- or I-shaped	H- or I-shaped	S-shaped	Simple or branched longitudinal
Egg gallery—location	Phloem, cambium	Phloem, cambium	Phloem, cambium	Phloem, cambium	Phloem, cambium
Manner of egg deposition	Individual egg niches	Individual egg niches	Individual egg niches	Individual egg niches	Eggs deposited in masses
Larval mines—location	Cambium-phloem	Cambium-phloem	Cambium-phloem	Cambium-phloem to outer bark	Cambium-phloem-middle bark
Larval feeding habit	Individual mines	Individual mines	Individual mines	Individual mines	Gregarious feeding
Pupal cell—location	Phloem and inner bark	Phloem and inner bark	Phloem and inner bark	Inner bark	Phloem and inner bark
Adult emergence habit	Several emerge through 1 hole	Several emerge through 1 hole	Several emerge through 1 hole	Individual exit holes	Several emerge through 1 hole
Days required for one complete generation	18-25	20-30	25-30	30-54	75-120
Generations per year	10 or more	6 or more	6 or more	3 to 5 or more	2 or more

row elevation on each side. The elytral declivity is convex. The sexes may be differentiated by the presence of a transverse elevation on the anterior area of the pronotum of the female *(16)*.

The insect is monogamous. It completes its life cycle within the bark of the host in 30 to 54 days. In the Deep South, activity often continues throughout the year.

First attacks on a tree usually occur on the mid-stem and are marked by whitish pitch tubes and red boring dust. If resin flow is abundant, initial burrows may be confined to the outer and middle layers of bark for some distance before they penetrate the inner bark. Initially attacking beetles are often "pitched out"—repelled by an excessive resin flow—but successive attacks usually overcome the host. Thereafter, or in the absence of a heavy resin flow during preliminary attacks, the beetles bore directly through the bark and the female constructs a small nuptial chamber in the phloem *(52, 66)*. The exact role of resin in overcoming early beetle attacks and the relation of multiple attacks to subsequent resin flow are inadequately understood. The rate at which gallery construction proceeds is apparently influenced by the amount of resin the adults encounter in the phloem-cambial area *(66)*.

Following fertilization by the male in the nuptial chamber, the female begins to excavate the egg gallery diagonally across the grain of the wood. Most mining is in the cambium and phloem, but the surface of the sapwood is etched faintly. The direction of the mining eventually is reversed, thus creating a typical S-shaped or serpentine pattern. The male follows the female and removes the boring particles *(35)*. When the beetles have excavated one or two inches of egg gallery, they construct a secondary opening radially to the bark surface and fill the main entrance and gallery to that point with borings. This process of making new openings to the surface and filling in the previous gallery is repeated at intervals of one-half to one or more inches as long as egg gallery excavation proceeds *(52)*.

Hopkins *(52)* reported that the female begins to deposit individual, pearly white eggs in small cavities in each side of the gallery about the time the first secondary opening is formed. Niches containing eggs usually are one-eighth to one or more inches apart. Eggs are held in place by fine, tightly packed borings. Each female deposits about 20 eggs *(75)*.

Eggs normally hatch in 3 to 9 days *(35)*. By pushing against the egg-securing material, the tiny larvae are able to bite into and enter the phloem. Tunnels constructed by early stage larvae are thread-like and visible when the inner bark is exposed. As the larvae develop, their tunnels are considerably enlarged and are usually concealed within the inner bark. Fronk indicates that there are four larval instars, the larval stage usually lasting 25 to 38 days. Completed larval mines are comparatively short, 5 to 20 mm. long *(66)*.

Prior to pupation, the larva extends an oval feeding area outward into the middle bark and parallel with the cambium. Usually the cell is large enough to break through the inner bark, although pupation may occur at various levels within the bark, apparently depending upon bark thickness. The pupal stage usually lasts 8 to 11 days.

Each adult constructs its own emergence hole, either directly from the pupal cell or—following a brief period of feeding—from a lateral gallery in the outer bark *(12)*. Parent adults frequently leave the host tree while their broods are still in the larval stage. They may reattack the same tree or fly to new trees as do some of the western bark beetles. Brood adults may emerge over a period of 10 to 32 days, depending in part upon the time elapsed between the laying of the first and last eggs *(66)*. A complete generation may develop in 30 to 54 days. Four complete generations and a partial fifth have been reported in West Virginia *(55)* and Virginia *(35)*, and 3 to 5 in western North Carolina *(11)*. Six or more generations appear possible in the lower South.

Early in the season, broods occur in all attacked trees except defoliated ones. During middle and late summer, most of the brood is gone from trees with yellow foliage and emergence is complete from red-topped trees. In southwest Mississippi and east Texas, broods emerge during late summer, prior to any apparent crown fading. Trees attacked in fall may remain green until spring. MacAndrews *(66)* found that, in western North Carolina, trees with yellow foliage contained the insect in the larval stage; those with sorrel foliage, larvae and pupae; and those with brown foliage, mature pupae and adults. This correlation

varies with season, probably with latitude and elevation, and with amount of blue stain.

Emerging broods may attack immediately adjacent trees or fly to stands some distance away. Trees under 15 years of age or 2 inches in diameter are rarely attacked, but outbreaks may develop in a wide variety of stands and sites *(7, 25, 55, 66)*. Spot kills of one-eighth to several hundred acres are characterized by a central area of defoliated trees, a surrounding zone of red-topped trees, and a perimeter of trees that have fading crowns or are still green, though infested. Infestations may extend in finger-like projections from the periphery.

Hopkins *(52)* and MacAndrews *(66)* report that the southern pine beetle exhibits a swarming habit. This observation is partially confirmed by the great numbers found on and around host trees during initial attack. Hopkins wrote that the beetles fly by night as well as by day, and that at times great swarms rise high in the air and are carried long distances by wind. Detailed information on this feature of the beetle's behavior is lacking.

Study of dispersal habits has been unsuccessful. Recent attempts to determine flight habits by releasing beetles treated with radioactive iridium failed for lack of a satisfactory technique for handling the insects between collection and release *(121)*.

The beetle overwinters in all stages of development, usually in single trees widely scattered around the periphery of active spot kills. Lack of crown discoloration often hinders detection until after broods have emerged.

Large and sudden population fluctuations characterize the southern pine beetle. Hopkins *(54)* believed that increases may be associated with varieties of the typical form which are able to extend their range into new areas or attack trees that would normally be resistant. Other workers feel that population increases are caused by environmental influences which have detrimental effects upon the host *(25, 26, 41, 42, 71)*. Fungus disease, parasitic nematodes, excessive rainfall, or low temperatures have been suggested as causes for sudden beetle declines *(8, 26, 33, 39, 52)*.

Observations by Lee *(62, 111)* indicate that, where populations are increasing, the beetles attack scattered groups of pines in young, dense stands. When an epidemic has developed, all age classes and densities are vulnerable. Where the population is declining, attacks are confined to scattered trees but under a wide variety of stand conditions. Lee also reported that infestations frequently occur in slow-growing stands.

Attempts to induce attack on standing trees or caged bolts have been extensive, varied, and never fully successful, though they have produced much useful information. In early experiments in the Southeast, effects of drought were simulated by trenching around pine trees and covering the soil with canvas. Data were taken on subsequent growth, sap density of the phloem and leaves, soil-moisture and temperature relationships, and susceptibility of trees to attack *(66, 90, 106)*. These and subsequent studies indicated that some abnormal physiological condition resulting from drought is essential for brood development *(25, 26)*; that beetles introduce blue stain spores into trees and create conditions favorable to stain development *(18, 19, 78)*; that the rapid death of trees may be directly attributed to blue stain fungi and yeasts, rather than to girdling of the inner bark *(18, 77)*; that the wood beneath beetle galleries dries from the outer ring toward the center of the trunk; that the blue stain fungus *Ceratocystis minor* (Hedgc.) Hunt [3] is closely associated with stoppage of conduction and drying of wood *(20)*; and that broods may be adversely affected by excessive moisture and extreme low temperatures *(8, 10, 29, 91)*.

The early studies suggested that some type of mechanical injury which would affect moisture content of the host would create conditions favorable for the beetle. In subsequent studies *(13, 29, 66, 86, 90, 91)* girdling, salting, scorching, and lodging generally failed to induce attack. Caging beetles on trees was unsuccessful because of difficulties in handling the insects. Caging infested bark on uninfested trees or logs induced emerging beetles to attack the new material. Trap-tree experiments indicated that growth retardation plus basal or mid-stem circumferential bark-stripping invited attack. Watering of trees, or complete defoliation by fire, caused heavy mortality of newly established broods, but pruning or topping had very little effect. Large tops, slash, and logs served as breeding sites where beetles were not nu-

[3] C. minor (Hedgc.) Hunt was previously described as **Ceratostomella pini** Rumbold.

merous enough to carry on their development in green trees.

During 1954-1958, several workers attempted to rear the insect under artificial conditions. Unsuccessful efforts included electrical "shocking" of bolts and introduction of blue stain fungi prior to exposure *(103)*. Osgood and Carter, after testing several techniques for rearing, concluded that poor development and low emergence were not correlated with degree of attack but with high moisture content in the wood and bark which caused heavy larval mortality *(82)*. Texas studies in 1958 and 1959 also resulted in poor brood development despite rather heavy attack, but were inconclusive regarding the role of host moisture content.

IPS Engraver Beetles

The three *Ips* species differ in detail, but are so similar in habits and life histories that they can be considered together. They have not been intensively studied and research may reveal behavioral patterns of use in control.

The posterior end of the adult's elytra is diagonally truncate and somewhat concave, and the exterior margins are lined with teeth. *I. avulsus* is 2.1 to 2.6 mm. long and has four teeth on each wing cover; *grandicollis,* 3.0 to 3.9 mm. long, has five; and *calligraphus,* 4.0 to 6.0 mm. long, has six (table 3). The males have coarser sculpture and greater development of the declivital teeth than do the females *(16)*.

Ips prefer recently killed trees and slash, but are capable of breeding in trunks and limbs of apparently healthy trees *(2)*. Infestations in green timber are usually sporadic and of short duration. Spot or group kills in pulpwood- or pole-size pines, or less often in mature stands, characterize outbreaks. As with the southern pine beetle, broods may develop rapidly enough in the summer to emerge shortly after or even before crowns begin to fade.

Season of activity corresponds with that of the southern pine beetle. Near the Gulf Coast, new attacks occur and established broods frequently become active during mild periods in winter.

Ips avulsus prefers stems less than 6 inches in diameter or the tops and branches of recently felled trees, and occasionally attacks tops of apparently healthy trees. When weather is adverse to tree growth, as during the severe drought in east Texas in 1956, *avulsus* may become a primary attacker, infesting the entire stems of large trees. Under other circumstances, it is a secondary invader of trees attacked by other insects or dying from other causes. *Ips grandicollis* prefers the stems of saplings or the upper stems and limbs of larger trees, though it may burrow in limbs less than 1 inch in diameter or in stumps of recently cut trees. *I. calligraphus,* the largest of the three southern species, occupies larger stems, usually above 6 inches in diameter. Chittenden *(24)* considered *I. grandicollis* as potentially very destructive to live timber.

Ips are polygamous. Three to 5 females and 1 male usually occupy each gallery. In all 3 species the male attacks first, boring a hole through the outer bark and constructing a small irregular nuptial chamber in the phloem. He initiates a series of egg galleries which are completed when the females arrive. These galleries radiate in all directions from the nuptial chamber through the phloem but eventually tend to run parallel with the grain of the wood to form a rough H or I shape. In the Gulf States, galleries of all 3 species are usually visible in the exposed inner bark surface. Haliburton reported that, in North Carolina, *avulsus* larval galleries are usually concealed within the inner bark *(37)*.

As the females continue the excavations, they deposit eggs individually in small niches at irregular intervals on both sides of the galleries and secure them with plugs of frass. A *calligraphus* female may lay 100 fertile eggs in one gallery *(37)*; comparable data for the other two species are not available. The larvae of all three species tunnel through the phloem until fully grown, when they hollow out cells in the inner bark and pupate. Number of larval instars is undetermined.

Callow or young adults feed beneath the bark before emerging. Several may emerge from a single hole *(11)*. Limited observations indicate that *calligraphus* may complete a generation in 25 days *(66)*, *grandicollis* in 20-25 days, and *avulsus* in 18-25 days. *Ips avulsus* may, therefore, have 10 or more generations a year, the two larger species 6 or more.

Ips overwinter in all stages in scattered single trees and recently cut logs and slash.

Black Turpentine Beetle

Until about 1949 the black turpentine beetle was considered relatively innocuous, rarely killing healthy pines *(60, 92)*. Today it is recognized as one of the most serious pests of partially cut stands. Its attacks are not always lethal, but the risk of losing high-value trees is enough to warrant prompt control wherever infestations are heavy.

The black turpentine beetle is the largest southern pine bark beetle, being 5.0 to 8.0 mm. long (table 3). The elytral declivity is convex. Females have broader, stouter, and more compressed antennal clubs than males, narrower heads, and smaller mandibles *(16)*. Additional diagnostic features are needed.

The species is active during most of the year in the southern part of its range, although somewhat restricted from December through March. Early in spring, large numbers of adults emerge and attack freshly cut stumps and the lower trunks of weakened trees. Occasionally stumps and apparently healthy trees are attacked simultaneously *(5, 65)*.

The beetle has occasionally been observed in swarms *(48, 52, 55)*. Greatest flight activity apparently occurs during late afternoon *(98)*.

Where trees are attacked, the larger ones are preferred. Initially, entries are usually on the lower 18 inches of the trunk and are few in number. Eventually they may occur 10 feet or more up the stem and on the larger lateral roots *(65, 98, 100, 102)*.

The insect is usually monogamous. Working in pairs, the adults bore through the bark to the soft phloem, at which point they excavate an egg gallery first above the entrance for a short distance, then downward in a general longitudinal direction. The gallery varies in length from 6 to more than 20 inches. It sometimes branches but usually is a simple tunnel with irregular widenings. At one or more of the widened areas the female deposits clusters of 50 to 200 eggs on a cushion of fine boring particles separated from the main gallery by a partition of similar material.

In the Gulf States the eggs hatch in about 10 days. Larvae feed gregariously in the soft inner bark for 5 to 7 weeks. The number of instars remains to be determined. Larvae from a single egg gallery may kill 2 square feet of bark. If several feeding areas join, the tree is girdled. The larvae pupate in individual cells beneath the bark, the pupal stage lasting 10-14 days. Callow adults feed beneath the bark until fully mature, then emerge through ventilating or exit holes.

In the Gulf States a generation may mature in 2½ to 4 months *(65)*. There are two and part of a third generations per year, with a complex overlapping. The insect overwinters in all stages of development, the adult apparently predominating.

Populations may develop rapidly following outbreaks of other bark beetles or extensive stand disturbances *(14, 55, 64, 65, 69, 100, 113, 117)*. Beetle activity and tree mortality usually begin the first year following such disturbances and generally subside after about 2 years; but in the naval stores region severe attacks may continue for 3 or more years *(98)*. Infestations usually are worst on poorly drained sites, although upland areas are by no means imune. Smith *(100)* found that 20 percent of the trees remaining after logging, burning, or turpenting may be attacked in a single season.

Interrelationships of Bark Beetles

A tree may be killed by the attacks of a single beetle species, but commonly two or more species are present. Quite typically the upper, central, and lower parts of a large tree may be attacked by the small, medium, and large *Ips*, respectively, or the southern pine beetle may be accompanied by one or more *Ips*. Similarly the black turpentine beetle may enter the bases of trees whose upper stems contain the southern pine beetle or *Ips*, or *Ips* may attack the upper stems of trees infested with the black turpentine beetle. Zones of occupancy often overlap completely, making it difficult to determine the primary attacker, the role of the various species in destruction of the host, or the extent to which the species support or impede each other.

The role of a species may vary from time to time. During epidemics, the southern pine beetle is typically the primary attacker *(47)*, but in South Carolina during 1955 *Ips calligraphus* and the southern pine beetle were equally represented in the central areas of infestations and the proportion of *Ips* in individual trees increased with distance from the infestation center *(73)*. Elsewhere in the Southeast these species have at times been equally abundant in individual trees *(66, 78)*.

Fiske and Snyder observed that *I. avulsus* was at times more destructive than the southern pine beetle, and noted instances in which *calligraphus* and the southern pine beetle entered trees following primary attacks by *avulsus.*[4] In 1955 and 1956, *avulsus* was found working alone in tops of green trees around the periphery of southern pine beetle infestations in Alabama *(114, 117, 119).* It was not determined whether *avulsus* was the primary insect or whether populations built up in trees infested by the southern pine beetle and then, by virtue of a shorter life cycle and in the absence of preferred breeding material, preceded the latter insect into green trees.

Beal and Massey *(12)* found the southern pine beetle breeding occasionally in windfalls, larger pieces of slash, and trees attacked by other insects, particularly *Ips.* This tendency was most pronounced during years when the insect occurred in limited numbers.

Ips and black turpentine beetle populations increase considerably during and after southern pine beetle epidemics *(62, 108, 109),* for trees infested by the southern pine beetle evidently are favorable breeding sites *(12).* The large populations of *Ips* and turpentine beetle then spread to nearby uninfested trees as their preferred host material becomes exhausted. During population increases, intra- and interspecies competition for food is thought to occur between developing broods *(102).* Such competition may reduce not only population potential but also the vigor of current broods.

ENVIRONMENTAL INFLUENCES

Forest Types and Conditions

Ips and the black turpentine beetle exhibit no preference for timber type but seem to be attracted to any stand in which some disturbance has left fresh pine slash, stumps, or weakened or injured trees. Stands of large trees on flat, poorly drained sites are particularly susceptible to the turpentine beetle, although similar stands on upland sites are by no means immune.

Hopkins *(55)* reported that mature old-growth pine was very attractive to the southern pine beetle. Most of the southern pine forest is now second growth, and this beetle attacks trees of practically all sizes *(12, 36, 43, 62, 70, 80, 87, 110).* It prefers dense pure stands of pulpwood and pole size, especially during epidemics *(11, 23, 36).* Beal and Massey *(12),* as well as Balch *(7),* refer to mixed pine-hardwood stands of the Piedmont and southern Appalachians as relatively free from attack. Observations in the flatwoods of southeast Texas tend to confirm a preference for pure stands, but enough attacks occur in mixed stands to suggest that the topic needs more investigation.

In the southern Appalachians, outbreaks of the southern pine beetle usually originate on ridges or other dry sites with south or west exposures. Most of the pine in the area is on such sites *(26, 29, 62, 70, 80).*

All the bark beetles are troublesome in the poorly drained bottoms and flatwoods of the Gulf Coast. Here root systems are shallow, and prolonged drought or flooding may weaken the trees seriously. The hazards are exemplified by the heavy *Ips* activity on flatwoods sites in east Texas at the height of the 1952-1956 drought and black turpentine beetle attacks over extensive areas flooded in northwestern Louisiana during 1957-1958 *(117, 119).*

A number of soil types have been associated with beetle infestations. From 1924-1931, drought augmented by bark beetle attack caused heavy pine mortality on the gumbo or clay subsoils characteristic of many Coastal Plain sites, and on shallow soils overlying limestone and solid clay hardpans *(21).* Infestations in mountainous and rolling hill areas of Alabama in 1953-1954 *(62)* occurred on sand or sandy loam soils underlain by a clay pan, or on sandy, rocky, or silt loam soils.

Stand Disturbances

Natural disturbances and the management, harvest, and utilization of southern pine forests frequently contribute to fluctuations in beetle populations.

[4] Unpublished reports, copies of which are on file at the Forest Insect Laboratory, Southern Forest Experiment Station, Gulfport, Mississippi:

Fiske, W. F. The destructive pine bark beetle in the southern states—a report of investigations made in cooperation with work at the Southern Field Station, Tyron, N. C., during the years 1903, 1904, and 1905.

Snyder, T. E. Brief summary of conditions as observed in South and North Carolina during the fall and winter of the 3rd year of invasion by D. frontalis. Report is dated January 1912, and covers period 1909-1911.

Lightning strikes are often the centers for localized beetle activity *(12, 41, 59, 107)*. Windfalls and pines damaged by ice or hail, particularly over extensive areas, are attractive to beetles *(12, 74, 104)*.

Pruning, thinning, and harvesting leave fresh stumps and tops and wound residual trees. Road building and grading, ditch-digging, plowing of fire lanes, and right-of-way clearing may alter soil and moisture levels and expose or damage roots. These conditions favor *Ips* and black turpentine beetles and may induce southern pine beetle attacks if this species is in the area.

Harvests in southern pine forests often involve successive operations for ties, cooperage, poles and piling, saw logs, and pulpwood; hardwood and pine components are usually removed separately. Skidding and hauling during each operation may compact soils, alter soil levels in relation to root systems, injure residual trees either above or below ground, concentrate infested logs or bolts near previously uninfested stands, and accumulate large quantities of fresh-cut material. After the cut material is exhausted, beetle populations frequently spread into residual trees *(6, 112, 120)*.

Tractor operations leave more injured trees than horse or mule logging. Furthermore, the larger and more powerful machines of recent years require more space and tend to be handled more carelessly than older, lighter equipment. Convergence of skidding trails, multiple relocation of roads, and deep rutting during wet weather all damage pines which then become attractive to beetles, particularly the black turpentine beetle *(6, 64, 65, 113, 119, 120)*.

Hopkins *(55)*, as early as 1909, pointed to the desirability of continuous rather than intermittent logging. He reported that, where new slash and stumps were continuously available, *Ips* and black turpentine beetles confined themselves to this material. When logging was suspended, they shifted to live trees. Other workers *(11, 105)* have confirmed these observations, and continuous operation is widely recommended to minimize *Ips* damage, especially in dry seasons.

Winter logging has also been proposed. It would seem advantageous for small tracts where continuous operation is infeasible, provided that the slash deteriorates before beetles begin their spring activity. On the other hand, winter logging on wet ground may compact soil and damage roots enough to create insect hazards which would offset possible advantages. Research on the possibilities is much needed.

Many wildfires and some prescribed burns damage main stems and surface roots and seriously defoliate groups of pine trees. Fires seem to be particularly harmful on sites where roots are close to the surface *(42, 116)*. Areas of concentrated fire damage often become starting points for *Ips* and southern pine beetle outbreaks *(109)*. This is particularly true where trees are weakened by fires but not severely defoliated *(12, 23, 30, 91)*.

St. George and Beal *(91)* found that trees severely defoliated by fire developed high inner-bark moisture contents which caused heavy mortality of southern pine beetle broods.

There are no reports of southern studies aimed at reducing bark beetle damage by silvicultural means, but it is widely recognized that forest management may greatly influence the activities of these insects. Management which exposes stands to minimum disturbance may minimize beetle losses. Many entomologists have indicated, however, that overstocked pure stands are prone to beetle epidemics, particularly in dry weather *(35, 62, 70, 116)*. Silvicultural systems that permit maximum forest production, recognize the capabilities of specific sites for such production, and keep insect losses at acceptable levels must be a goal of future research.

Moisture and Temperature

Observations throughout the South have related drought to increases in bark-beetle activity *(26, 42, 71, 115)*. Some workers propose that drought occasionally has been the primary cause of heavy pine mortality and that beetles merely assisted in killing the trees *(21, 27)*.

Others point out that excessive precipitation may weaken trees, making them attractive to bark beetles *(41, 42)*. At least three outbreaks of the southern pine beetle since 1890 have developed during excessively wet periods following drought *(26, 117, 119)*. On the other hand, heavy rains may kill beetles in flight *(8, 12, 26, 102)*.

Early research in the Southeast indicated that moisture content of trees has a marked

effect on establishment and development of broods *(13, 25, 29, 78, 88, 90)*. After 4 or 5 weeks, depending on severity of attack, there is a definite increase in moisture content of the sapwood at the base of the tree, a reverse situation from that in unattacked trees. This reversal was ascribed to interruption in conduction of water from the roots and to rapid drying of tops by continuing transpiration. Phloem moisture followed a pattern similar to that in the wood but usually was 10 to 20 percent higher. In severely defoliated or decapitated trees, increase in phloem moisture materially checked development of young broods *(91, 94)*.

R. W. Caird *(20)* found that the outer three rings of an attacked tree ceased to conduct moisture in 3 to 5 days, depending upon the severity of attack. Extensive tunneling in the phloem exposed the surface of the wood to the outer atmosphere through open entrance and ventilation holes. By stopping conduction, associated fungi apparently accelerated the rate at which the tree died.

Mild winters favor beetle populations by prolonging their active season—an example is the southern pine beetle activity in southeast Texas which continued throughout the winter 1959-1960 *(12, 52, 65, 70, 71, 123)*. St. George and Beal *(91)* determined that eggs and some pupae of the southern pine beetle could survive -5° F. In other studies, air temperatures from -5° to 10° F. damaged all stages except the egg *(8, 10)*. Mortality was heaviest in the moist inner bark *(81, 91, 107, 119)*. Bark has insulating value, and its thickness may affect brood survival during unusually cold periods.

No instances of lethal high temperatures in standing beetle-infested trees have been reported, but several workers have indicated that exposed sides of felled products reach temperatures fatal to *Ips* and southern pine beetles.

Host Physiology

Most research on host-insect relationships has been concerned with attacks on weakened or recently dead trees and cut products. While stand disturbances appear to be related to successful attack, the specific host conditions associated with such attacks, and the reasons why beetles select apparently healthy hosts, are little understood.

Early explanations of host-beetle relationships centered around the theory that "sap flow" helped to determine success of attacks by the southern pine beetle. Hopkins *(52)* suggested that by late July "sap flow" was less profuse and that, if southern pine beetles were numerous, they would attack living trees. He felt that preliminary attacks were concentrated in the central portion of the trunk because there was less "resistance" to injury in this zone than in the lower stem.

MacAndrews *(66)* supplemented Hopkins' assumptions as to the influence of moisture and resin on establishment of southern pine beetle broods. He reported that initial attacks drained resin supplies enough to permit later attacks to succeed. No measurements of resin flow were made. Lee and Smith *(65)* found that the quantity of gum produced by a tree had little effect on its resistance to the black turpentine beetle. In *Ips* species, which are polygamous, loss of considerable numbers of males in unsuccessful initial attacks would still leave enough to fertilize the entire female population *(37)*.

Bark thickness apparently influences the location of attacks and the survival of broods *(29, 37, 66, 79, 91)*. An outstanding example is the black turpentine beetle's selection of the thick-barked basal portion of the trunk and the main roots of trees. Attacks by the two larger *Ips* species and the southern pine beetle occur in the lower three-quarters of the main stem, where larger populations may successfully complete development than would be possible beneath the thinner bark of tops and small limbs. Because of its small size, *I. avulsus* is able to develop and multiply rapidly in thin-barked upper stems and branches.

ASSOCIATED FORMS AFFECTING BEETLE POPULATIONS

Fungi

The southern pine beetle and *Ips* beetles introduce staining fungi and yeasts into the trees they infest *(18, 19, 32, 77, 78, 84, 125)*. Associated mites also seem to disseminate the fungi *(41)*.

Nelson *(77)* believed that southern pine beetle broods would be unable to develop in the phloem were it not for the rapid establishment of staining fungi which, in his opinion, killed the tree. Bramble and Holst *(18, 19)* and

Holst *(45)*, on the other hand, found no evidence that the fungi generally associated with southern pine beetles are essential for beetle development from the egg stage. They indicated that the fungi do no more than assist in killing beetle-attacked trees.

Ceratocystis minor (Hedgc.) Hunt or *C. ips* (Rumbold) C. Moreau, *Pichia pini* (Holst) Phaff,[5] and an unnamed basidiomycete are the first forms to attack the sapwood following beetle entry *(18, 19, 44, 83, 84)*. *C. minor* is specifically associated with the southern pine beetle and *C. ips* with *Ips* engraver beetles. *Dacromyces* sp. and *P. pini* penetrate outer sapwood rings rapidly during the first week of beetle attack. During the second week, *C. minor* or *C. ips* penetrates as deeply as the primary forms; these two blue stain fungi are the prominent micro-organisms in the sapwood during the final stages of beetle attack.

Penetration by fungi is accompanied by a gradual drying of the sapwood—the result of continuing transpiration by the crown while the infected stem is losing its ability to transmit water from the roots. The result is the reversed moisture situation described by Beal and St. George *(13)*.

At least some of the fungi discussed above are capable of killing trees by themselves *(77, 78)*. However, they are disseminated mainly by insects, require some type of mechanical injury as an infection court in the host, and must encircle the stem before mortality ensues *(18)*. Death from blue stain following unsuccessful beetle attacks, if it occurs at all, is a slow process because of the limited number of beetle contacts with the sapwood *(32)*.

Limited observations indicate that other fungal forms sometimes influence the susceptibility of pines to beetles. Hetrick *(41, 42)* noted several instances where trees infested with the southern pine beetle also had rhizomorphs of the mushroom root rot *(Armillaria mellea* (Vahl.) Quel.) between the bark and sapwood near the groundline. Callus sapwood at points where the fungus mycelium was growing upward clearly indicated that fungus development had preceded beetle attack.

Hopkins *(51)* found evidence that disease reduced southern pine beetle populations in an outbreak area in the central Atlantic States in the early 1890's. A fungus associated with the beetle was later placed in the Family Tuberculaniaceae and named *Cylindrocola dendroctoni* Peck *(52)*.

Snyder[6] observed a parasitic fungus common in the pupal cells of the southern pine beetle, *Ips avulsus*, and *I. calligraphus*. Later, Harrar and Ellis *(38)* and Hetrick *(40)* found an entomophagous fungus of the genus *Beauvaria* which was pathogenic to healthy southern pine beetle larvae and caused high mortality of overwintered broods.

Conditions under which pathogenic fungi and virus organisms develop and reduce beetle populations require considerable study. Research to determine pathogenic organisms other than those presently known is also needed.

Insects

Various insects are associated with all of the southern bark beetles. Many are parasites, hyperparasites, and predators (tables 4, 5). Others are scavengers or competitors for food, and still others are responsible for the initial deterioration of the host plant (table 6).

Most insect parasites are small wasps and flies.

A few species deposit their eggs in the host egg galleries or larval mines; the parasite larvae seek their host after hatching. Some oviposit through the bark, while micro-forms commonly enter the galleries of the host. The parasites usually spend their lives in or on the body of a single host, ultimately causing its death. Fiske *(34)* found that 45 percent of the southern pine beetle larvae in the upper thin-barked zone of the main stem were parasitized by braconids, whereas the same group was unable to parasitize larvae beneath the thicker bark of the lower stem.

The most important predators are beetles and piercing and sucking insects. Very little has been published on the habits and role of these forms, except for the clerids and ostomids, two predatory beetle families. As early as 1893, Hopkins *(49)* determined that *Clerus quadrisignatus* var. *nigripes* Say and *Thanasimus dubius* Fab. are predaceous on *Ips grandicollis* and that *T. dubius* also attacks *Ips calligraphus* and the southern pine beetle. He im-

[5] P. pini (Holst) Phaff was previously described as Zygosaccharomyces pini Holst.
[6] Snyder, T. E. 1912. Brief summary of conditions as observed in South and North Carolina during the fall and winter of the third year of invasion by Dendroctonus frontalis. Unpublished memo to files. U. S. Dept. Agr., Bur. Ent.

Table 4.—*Insect parasites of the southern pine bark beetles*

Parasite family and species	Host and stage parasitized
Braconidae	
Bracon pissodis Ashm. *(49, 50, 52)*	Southern pine beetle—larva and pupa
Coeloides brunneri Vier. *(22)*	*Ips calligraphus*
Coeloides pissodis (Ashm.) *(22, 35, 39)*	Southern pine beetle
Compyloneurus (Bracon) mavoritus (Cress.) *(22)*	Southern pine beetle
Dendrosoter sulcatus Meus. *(39, 76)*	Southern pine beetle *I. avulsus*
Doryctes sp. *(22)*	Southern pine beetle
Ecphylus (Sactopus) schwarzii (Ashm.) *(22)*	Southern pine beetle
Heydenia unica C. and D. *(22, 39, 49, 50, 52)*	Southern pine beetle—larva and pupa
Lochites sp. *(49, 50, 52)*	Southern pine beetle—larva and pupa *I. grandicollis*—larva and pupa *I. calligraphus*
Spathius canadensis Ashm. *(22, 39, 49, 50)*	Southern pine beetle *I. grandicollis*
Spathius pallidus Ashm. *(22, 49, 50, 52)*	*I. grandicollis*—larva
Dolichopodidae	
Medetera sp. *(35)*	Southern pine beetle
Eulophidae	
Tetrastichus thanasimi Ashm. *(52)*	*Thanasimus dubius*
Pteromalidae	
Cecidostiba dendroctoni Ashm. *(22, 35, 39, 52)*	Southern pine beetle *I. grandicollis*
Tomicobia tibialis Ashm. *(22, 52)*	*I. grandicollis* *I. calligraphus*—adult
Stratiomyidae	
Microchrysa polita (L.) *(35)*	Southern pine beetle
Tachinidae	
Tachina sp. *(52)*	*Thanasimus dubius*
Torymidae	
Roptrocerus (Pachyceras) eccoptogasteri Ratz. *(22, 39, 52)*	Southern pine beetle—larva and pupa *I. grandicollis*—larva and pupa *I. calligraphus*—larva and pupa

ported large numbers of a closely allied predator, *Thanasimus formicarius* (F.), from Europe for use in controlling the southern pine beetle *(46, 52)*, but an outbreak in the central Atlantic States (table 1) ended before the value of this predator could be determined.

Subsequent observations throughout the South indicated that larvae of predaceous clerids and ostomids feed on the eggs, larvae, pupae, and callow adults of *Ips* and the southern pine beetle in and beneath the bark. Adults of these predators also destroy large numbers of adult bark beetles as they attack green trees *(28)*. The effectiveness of these insects in widespread biological control is as yet undetermined, although they have been observed in great abundance in several beetle outbreak areas.

While little is known about the influence of environment on associated insects, clerid and ostomid larvae have been observed to survive temperature drops to 0° F. while bark beetle broods suffered heavy mortality *(107, 119)*. Low temperatures may thus favor biological control by increasing the predator-bark beetle ratio.

Insect competitors for food limit bark beetle populations, but their overall influence is un-

known. A possible exception is the relation of cerambycid larvae to bark-beetle development. Adults of *Monochamus titillator* (F.), *Acanthocinus nodusus* (F.), *Stenocorus lineatus* Oliv., and *Xylotrechus sagittatus* (Germ.) oviposit in the bark at or very soon after initial attack by the southern pine beetle and *Ips*. Oviposition may continue for 10 days. Larvae of these wood and bark borers develop rapidly and may mine so extensively that bark beetle broods are destroyed directly or starve because their phloem food supply has been consumed *(66, 73)*. If larvae of the southern pine beetle begin mining before or immediately after cerambycid larvae become active, however, they may subsist in outer layers of the bark in thick-barked trees where wood-borer larvae do not feed.

Smith and Lee *(102)* observed that competition for food with wood destroyers killed some black turpentine beetle larvae.

Despite these interrelationships, there is no record that bark beetle broods have ever been completely destroyed by predators, parasites, or competitors.

Table 5.—*Insect predators of the southern pine bark beetles*

Predator family and species	Host and role of predator
Anthocoridae	
Anthocoria sp. *(52)*	*Ips grandicollis* *I. calligraphus*
Lyctocoris elongatus (Reuter) *(35)*	Southern pine beetle. Nymphs and adults feed on eggs and larvae
Scoloposcelia flavicornis (Reuter) *(35)*	Southern pine beetle. Nymphs and adults feed on eggs and larvae
Cleridae	
Enoclerus quadriguttatus Oliv. *(22)*	Southern pine beetle
Enoclerus quadrisignatus var. *nigripes* Say *(22, 49, 52)*	*I. grandicollis*
Priocera castanea (Newman) *(17)*	Southern pine beetle
Thanasimus dubius (F.) *(17, 34, 35, 49, 52)*	Southern pine beetle and 3 *Ips*. Larvae feed on eggs and larvae, adults on adults
Elateridae	
Elaterid sp. *(22, 52)*	Southern pine beetle and black turpentine beetle —larvae feed on larvae, pupae, young adults
Histeridae	
Cylistix cylindrica (Payk.) *(22)*	*I. grandicollis* *I. calligraphus*
Hister cylindricus Payk. *(49, 52)*	*I. grandicollis* *I. calligraphus*
Ostomidae	
Temnochila virescens (F.) *(35)*	Southern pine beetle. Larvae feed on larvae and pupae, adults on adults
Staphylinidae	
Gryohypnus (Xantholinus) emmenus (Grav.) *(22)*	*I. calligraphus*
Tenebrionidae	
Hypophloeus parallelus Melsh. *(49)*	Southern pine beetle *I. grandicollis*
Hypophloeus tenuis Lec. *(22, 52)*	*I. calligraphus*
Tenebroides collaris (Strum) *(35)*	Southern pine beetle. Larvae feed on larvae and pupae, adults on adults

Nematodes and Mites

High mortality of southern pine beetle broods has been noted where nematode and mite species were associated with beetles in egg through adult stages *(35, 39, 67)*. The value of these associates for biological control has not been appraised. A list of the forms follows:

Nematodes

Genus *Anguillonema:* endoparasitic on southern pine beetle

Genus *Aphelenchoides*

Aphelenchulus barberus Massey: males nonparasitic, females parasitic on southern pine beetle

Aphelenchulus gradicollis Massey: associated with *Ips grandicollis*

Mites

Family Parasitidae, *Parasitus* sp.: feed on southern pine beetle larvae

Family Uropinae, *Uropoda* sp.: heavy infestations prevent southern pine beetle flight

Family Dameosmidae

Family Cheltidae, *Cheltia* sp.

Family Laelaptidae, *Dendrolaelaps* sp., *Zercoseius* sp.

Family Acaridae, *Histiogaster carpio* (K.): feed on southern pine beetle larvae

Family Oribatoidae

Woodpeckers

Woodpeckers are commonly observed on beetle-infested trees. In seeking larvae, pupae, and adults of the southern pine beetle, woodpeckers frequently remove so much outer bark that sawlog-size trees assume a distinguishing buckskin or reddish-brown appearance *(36)*. Some of the bark fragments that fall to the ground are so large that beetles in them can still complete their development. Osgood *(107)* found that 77 percent of the southern pine beetle larvae remaining in the bark of "woodpeckered" trees were killed by low winter temperatures as opposed to 44 percent in trees not worked by woodpeckers. Smith and Lee *(102)* observed that woodpeckers exercise no appreciable control in the thick-barked basal portion of trees or stumps occupied by the black turpentine beetle.

Woodpecker activity is usually seasonal, reaching its peak in winter, and limited to occasional trees. The birds have their greatest value when infested trees are so few that most of the broods can be destroyed.

CHEMICAL CONTROL

For many years, standard recommendations for controlling bark beetles were to utilize infested trees as rapidly as possible; burn the slabs, tops, and unmerchantable infested trees; and peel and burn bark from stumps and unused logs *(4)*. Chemicals have facilitated immediate control where such methods have proved too costly or slow for such aggressive insects as the southern pine beetle. In addition, it has been found that many trees infested with the black turpentine beetle can be saved by timely spraying.

Early researchers attempted to introduce poisons into the sap-stream, the object being a low-cost application that would destroy the insects regardless of the effect on the trees *(13)*. Sodium arsenite, mercuric chloride, ammonium fluoride, sodium fluoride, carbon disulphide, hydrocyanic acid gas, and ethyl monodichloroacetate all reduced or destroyed broods, but only when applied on newly attacked trees and before conduction ceased *(9, 13, 31, 91, 93)*. The saw-kerf or saw-cut injection method *(3)* proved most suitable.

Limited tests of sprays were undertaken by St. George *(89)* in 1932. Kerosene injured and often killed pines. Orthodichlorobenzene destroyed broods and prevented further attack, although infested trees were seldom saved.

Experiments by western forest entomologists led to the development of a mixture of orthodichlorobenzene and fuel oil (1:5). The formulation controlled the mountain pine beetle *(95)*, and was successfully used on the southern pine beetle during the 1940's.

In 1950, Morris *(75)* demonstrated that broods of the southern pine beetle can be destroyed and the insect's spread prevented by spraying infested trees with 0.25 percent gamma isomer of benzene hexachloride in No. 2 fuel oil. Later studies in western North Carolina *(122)* indicated that a 0.5 percent spray was even more effective in killing either broods beneath the

Table 6.—*Insect competitors and scavengers associated with the southern pine bark beetles*

Associated insect family and species	Primary insect	Role
Buprestidae		
Buprestis apricans Hbst. *(28)*	Southern pine beetle	Competitor for phloem food supply
Cerambycidae		
Acanthocinus nodosus (F.) *(29, 66, 73)*	Southern pine beetle	Do.
	Ips grandicollis	Do.
	I. calligraphus	Do.
Asemum moestum Hald. *(29)*	Southern pine beetle	Do.
Astylopsis (Leptostylus) guttata (29)	Southern pine beetle	Fungal spore feeder
Monochamus titillator (F.) *(13, 66, 73, 90)*	Southern pine beetle	Competitor for phloem food supply
	I. grandicollis	Do.
	I. calligraphus	Do.
Stenocorus lineatus Oliv. *(73)*	Southern pine beetle	Do.
	I. grandicollis	Do.
	I. calligraphus	Do.
Xylotrechus sagittatus (Germ.) *(29, 73)*	Southern pine beetle	Do.
	I. grandicollis	Do.
	I. calligraphus	Do.
Colydiidae		
Aulonium tuberculatum Lec. *(52)*	*I. grandicollis*	Scavenger
Cucujidae		
Laemophlaeus testaceus Fab. *(52)*	*I. grandicollis*	Scavenger
Curculionidae		
Cossonus corticola Say *(28)*	Southern pine beetle	Do.
	I. grandicollis	Do.
	I. calligraphus	Do.
Pachylobius picivorus Germ.	Black turpentine beetle	Competitor for phloem food supply
Pissodes nemorensis Germ.	*I. calligraphus*	Do.
Histeridae		
Hister lecontei Mars. *(52)*	*I. calligraphus*	Predator
Hister parallelus Say *(52)*	*I. calligraphus*	Do.
Plegaderus transversus Say *(28)*	*I. grandicollis*	Do.
	I. calligraphus	Do.
Lathridiidae		
Corticaria elongata Hum. *(49, 52)*	*I. calligraphus*	Unknown
Nitidulidae		
Colastus unicolor Say *(49)*	*I. calligraphus*	Feeds on decaying and fermenting juices beneath bark

Table 6.—(Continued)

Associated insect family and species	Primary insect	Role
Ostomidae		
Corticotomus cylindricus (Lec.) *(28, 49, 52)*	*I. grandicollis*	Predator on ambrosia beetles, Cossonids
Platypodidae		
Platypus flavicornis Fab.	Black turpentine beetle	Pinhole borer in sapwood
Rhinotermitidae		
Reticulitermes flavipes Kol.	Southern pine beetle	Wood feeder
	Black turpentine beetle	Do.
Scolytidae		
Crypturgus alutaceus Sz. *(28, 73)*	Southern pine beetle	Competitor for phloem food supply
	I. grandicollis	Do.
	I. calligraphus	Do.
Hylastes sp.	Black turpentine beetle	Do.
Hylurgops glabratus (47)	Black turpentine beetle	Do.
Orthotomicus caelatus Eichh. *(15)*	*I. grandicollis*	Do.
	I. calligraphus	Do.
	Black turpentine beetle	Do.
Pityogenes meridianus Blkm. *(15)*	*I. avulsus*	Do.
Pityogenes plagiatus Lec. *(15)*	*I. avulsus*	Do.
Pityophthorus annectens Lec. *(15)*	*I. avulsus*	Do.
Pityophthorus bellus Blkm. *(28, 73)*	Southern pine beetle	Competitor for phloem food supply
	I. grandicollis	Do.
	I. calligraphus	Do.
Pityophthorus granulatus Sw. *(15)*	*I. avulsus*	Do.
Pityophthorus lautus Eichh. *(15)*	*I. avulsus*	Do.
Pityophthorus nudus Sw. *(15)*	*I. avulsus*	Do.
Pityophthorus pulicarius Zimm. *(15)*	Southern pine beetle	Do.
	I. avulsus	Do.
	I. grandicollis	Do.
Pityophthorus pullus Zimm. *(15)*	*I. avulsus*	Do.
	I. grandicollis	Do.
Xyleborus confusus Eichh. *(15)*	Black turpentine beetle	Pinhole borer in wood
Staphylinidae		
Xantholinus emmesus Grav. *(52)*	*I. calligraphus*	Scavenger or predator
Tenebrionidae		
Corticeus glaber Lec. *(28)*	*I. avulsus*	Plant feeder
Corticeus parallelus Melsh. *(28)*	Southern pine beetle	Do.
Corticeus piliger Lec. *(28)*	*I. calligraphus*	Do.
Trogositidae		
Trogosita virescens Fab. *(52)*	*I. calligraphus*	Unknown

bark or emerging beetles. However, the lower concentration continues to yield acceptable results and is widely used throughout the South. The spray is applied until the bark is dripping wet or at the rate of approximately 1 gallon per 100 square feet of bark surface. The long residual life of the chemical permits control crews to treat infested trees over extensive areas ahead of salvage units or to leave treated logs in the woods during adverse weather or under other conditions which prohibit salvage.

Also in 1950, tests of BHC for control of the black turpentine beetle were undertaken by J. F. Coyne, as reported by Lee and Smith *(65)*. As this insect occupies the thick-barked basal portion of trees and broods mature more slowly than those of the southern pine beetle, a stronger concentration with a long residual life was necessary. A spray of 0.5 percent gamma isomer of BHC in fuel oil proved highly effective when applied at the rate of 1 gallon to 40 or 50 square feet of bark. The addition of 3 pounds of ethylene dibromide to 5 gallons of spray improved control but not enough to justify the increased cost.

Stronger concentrations of BHC were more effective in killing the black turpentine beetle *(96, 97)*. A 1.0 percent concentration reduced tree mortality from the turpentine beetle by as much as 90 percent, as compared with unsprayed check trees *(101)*. Removal of duff and loose bark plates also aided in killing turpentine beetles inhabiting the thick bark of the lower stem and large roots.

In 1954 experimental spraying of the basal 20 to 25 feet of fire-scorched loblolly and shortleaf pines with BHC in fuel oil was found to reduce attacks by the large *Ips* species for several months *(63)*. Because attacks by *I. avulsus* occur on the upper stem, it is difficult to control this group in standing trees, but the treatment has been effective in cut logs or slash and is sometimes used where large populations develop in logging debris and threaten residual trees.

BARK-BEETLE RESEARCH NEEDS IN THE SOUTH

Necessary research on bark beetles that attack southern pines falls into two broad categories:

1. Basic research, primarily in insect and plant physiology and in insect biology and ecology, aimed at securing fundamental knowledge of the immediate environmental factors affecting bark beetles and their interrelationships.

2. Applied research into chemical, biological, and silvicultural means of dealing with the bark beetles.

Past study of forest insects has amply justified itself by the practical controls that have been developed, but the present lack of basic information sharply handicaps further applied research.

The following analysis of research needs has been prepared chiefly from the standpoint of the Southern Forest Experiment Station and its area of responsibility, but no single organization is likely to have the resources to cope with the job in its entirety. Much that is contemplated in the following paragraphs can and should be accomplished by Federal, State, and private research agencies, educational institutions, specialized laboratories, and other groups within the range of the southern pine bark beetles. The proposals stress the importance of basic knowledge from which practical controls can be developed. Often both basic and applied research are described or implied under the same subject heading.

Insect Biology and Physiology

Basic to progress in beetle control is thorough knowledge of the insects. Although more is known about the southern pine beetle than the other species, detailed research on all 5 beetles is needed, specifically:

> Each species' habits of mating, gallery excavation, oviposition, and brood development.
>
> Effects on all beetle stages of variations in temperature, humidity, resin production, moisture and nutrient content of the phloem, and other environmental factors.
>
> Techniques for rearing the southern pine beetle artifically, to facilitate detailed biological and physiological research.
>
> Flight and dispersal habits of the 5 species. Techniques for rearing and handling large populations, and for

using radioactive tracers and other aids.

Variations in life histories which may be related to climatic differences and locations. Such studies are particularly needed in the Gulf South.

Possible genetic variations which may be related to population fluctuations, especially of the southern pine beetle.

Host Physiological Relationships

Research in plant physiology as it relates to bark beetle populations should include the following basic studies:

Conditions or processes in the host which predispose a tree or stand to initial or continuing attack and favor or oppose successful brood development. Examples are the effect of resin and sap flow, physical and chemical characteristics of sap and resin, presence of fungi and bacteria, growth rate, bark thickness, and possibly other measurable factors of host physiology.

Root development and possible relationships between condition of roots and beetle attack. Many initial buildups may be associated with root deterioration caused by adverse weather, site, nematodes, or root-rot fungi.

Morphological and physiological features of host which influence effectiveness of associated forms as control agents.

Effect of seasonal variations in rainfall and temperature on host resistance.

Associated Forms Affecting Bark Beetles

Appraisal of the control value of pathogenic fungi, parasites, and predators should include the following studies:

Isolation and identification of entomophagous fungi.

Pathogenicity of entomophagous fungi to various beetle stages.

Conditions necessary for optimum development and effectiveness of pathogenic fungi.

Isolation and identification of predators and parasites capable of materially affecting beetle populations, and detailed study of their life histories and environmental requirements to determine their utility as substitutes for chemicals.

Relationships between and within bark beetle species and associated inner bark forms during epidemic and endemic periods.

Usefulness of woodpeckers in direct control or in altering the beetles' environment until they succumb to other environmental influences.

Silvicultural-Management Relationships

Research on silvicultural means for reducing losses from bark beetles should include:

Stand density or basal area as it relates to beetle populations. Long-term studies should be undertaken in areas where bark beetles have frequently been a problem.

Consideration of a beetle risk-class system for southern pine forests. The tree-age classes that are most susceptible in the West are lacking in the South, and the possibilities for a southern system have hardly been explored.

Merits of a single continuous operation for harvesting all wood products, as opposed to separate operations for individual products.

Logging techniques that minimize insect damage to residual stands. E. g., tree-length versus log-length skidding, need for follow-up sanitation cuttings, relation of beetle attack to season of cut on upland and flatwood sites, damage to residual stands as related to type of logging equipment, and preventive spraying of injured residuals.

Effect of cutting systems—seed tree, shelterwood, and clear-cutting in

strips—on susceptibility of residual stands under various weather conditions.

Relation of beetle damage to density and proportion of hardwoods in mixed stands.

Chemical Control

In the absence of more complete knowledge, chemicals are frequently the only means for combating beetles. Research should include:

Continued screening of insecticides to secure economical control with minimum damage to other organisms.

Continuing study to improve formulations, application methods, equipment, and timing. The importance of treating certain portions of beetle-infested trees has recently been questioned, particularly in the case of the black turpentine beetle. Refined criteria are urgently needed for selecting trees to be sprayed or salvaged.

Confirmation of recommended dosages for both preventive and remedial control.

Effect of insecticides on parasites and predators, and ways of modifying control procedures to favor these forms.

Biological Appraisals and Economic Evaluations

Research on appraisal survey techniques should seek to develop:

Systematic and quantitative techniques for evaluating trends in bark beetle populations.

A technique for appraising effectiveness and population trends of known parasites, predators, and other natural control agents.

A system for determining effectiveness of chemical control and the need to continue direct control—i. e., a sampling procedure for measuring mortality of existing beetle broods and rate at which new infestations occur.

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OCCASIONAL PAPER 180

SOUTHERN FOREST EXPERIMENT STATION
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